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Trait similarity patterns within grass and grasshopper communities: multitrophic community assembly at work

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Abstract. Trait-based community assembly theory suggests that trait variation among co-occurring species is shaped by two main processes: abiotic filtering, important in stressful environments and promoting similarity, and competition, more important in productive environments and promoting dissimilarity. Previous studies have indeed found trait similarity to decline along productivity gradients. However, these studies have always been done on single trophic levels. Here, we investigated how interactions between trophic levels affect trait similarity patterns along environmental gradients. We propose three hypotheses for the main drivers of trait similarity patterns of plants and herbivores along environmental gradients: (1) environmental control of both, (2) bottom-up control of herbivore trait variation, and (3) top-down control of grass trait variation.

To test this, we collected data on the community composition and trait variation of grasses (41 species) and grasshoppers (53 species) in 50 plots in a South African savanna. Structural equation models were used to investigate how the range and spacing of within-community functional trait values of both grasses and their insect herbivores (grasshoppers; Acrididae) respond to (1) rainfall and fire frequency gradients and (2) the trait similarity patterns of the other trophic level.

The analyses revealed that traits of co-occurring grasses became more similar toward lower rainfall and higher fire frequency (environmental control), while showing little evidence for top-down control. Grasshopper trait range patterns, on the other hand, were mostly directly driven by vegetation structure and grass trait range patterns (bottom-up control), while environmental factors had mostly indirect effects via plant traits. Our study shows the potential to expand trait-based community assembly theory to include trophic interactions.

Key words: abiotic filtering; bottom-up control; community assembly; competition; functional diversity; grasses; grasshoppers; herbivores; savannas; top-down control; trait dispersion; trophic interactions.

INTRODUCTION

Inspired by Jared Diamond's original idea of trait-based "assembly rules," many ecologists have adopted a trait-based approach in order to search for common principles in the assembly of local communities. According to this approach, the processes governing community assembly can be seen as "filters" that either allow or exclude species with certain functional traits from a species pool to enter a local community (Diamond 1975, Drake 1991, Weiher and Keddy 1995, McGill et al. 2006). Two processes are classically considered to be central in trait-based community assembly: abiotic filtering, that is, the exclusion of species that do not tolerate a particular abiotic stress (such as high temperatures), and competition or biotic filtering, that is, the exclusion of inferior competitors (Weiher and Keddy 1995, Weiher et al. 1998). Both these processes operate through functional traits that do

or do not allow a species to survive and successfully compete in a community, consequently resulting in nonrandom patterns of within-community trait similarity (Weiher et al. 2011). The effects of these processes on trait variation are generally expected to be opposite, with abiotic filters causing more restricted trait ranges among co-occurring species than expected by chance (hereafter called trait underexpansion, Fig. 1A) (Weiher and Keddy 1995, Weiher et al. 1998, Cornwell and Ackerly 2009), while competitive exclusion of species with too similar niches results in communities of species with a higher spacing of trait values than expected by chance, hereafter called trait overdispersion (MacArthur and Levins 1967, Pacala and Tilman 1994, Cornwell and Ackerly 2009; but see Scheffer and van Ness 2006, Mayfield and Levine 2010) (Fig. 1A).

Over the last decades, the effects of these filters on trait similarity patterns have been studied in various ecosystems and species groups, with mixed results, varying from random trait variation in communities, trait overexpansion, and trait underdispersion (reviewed in Weiher et al. 2011). These contrasting outcomes can

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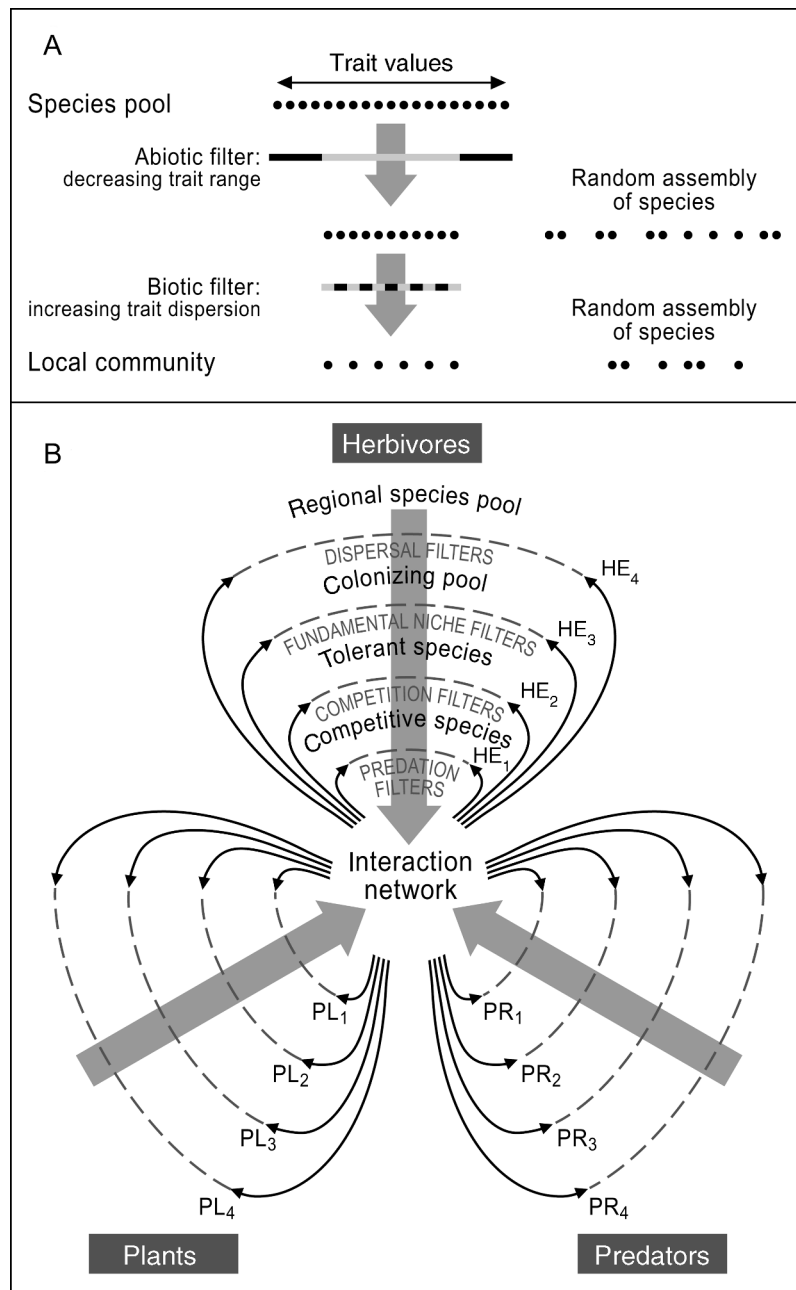


FIG. 1. (A) The classic conceptual idea for the assembly of communities sensu Diaz et al. (1998) and Weiher et al. (1998). On the left, the community is formed through an abiotic filter and resource partitioning while, on the right, a random selection of species from the species pool assembles in the community. The abiotic filter allows only species with trait values within a certain range that is smaller than the trait range of randomly assembled species, resulting in trait underexpansion. Competition and the consequent resource partitioning between species results in a relatively large evenness of trait distances within this range (hereafter trait overdispersion), compared with the trait distance of randomly assembled communities. (B) A newly proposed multitrophic extension of community assembly theory. This figure depicts community assembly at three trophic levels: producers, herbivores, and predators. Here, the process of community assembly goes through a dispersal, fundamental niche, competition, and predation filter. These filters determine which species can coexist in the local community or “interaction network.” They visualize if the occurrence of a species is restricted by its ability to sufficiently disperse, find its basic resources and tolerate the prevailing abiotic conditions, compete for resources, and withstand predators and diseases. The interaction network that results from these filters is not a static result, but shows a feedback on them. For example, by providing shelter, the presence of certain plant species may affect fundamental niche filtering of herbivores. Also, predation or herbivory may influence competitive filtering between plants or herbivores, respectively.

arise because of differences among habitats in the extent to which different community assembly processes dominate (Pausas and Verdu 2008, Cornwell and Ackerly 2009, Anderson et al. 2011) or because different processes act upon the assembly of different traits (Prinzing et al. 2008, Ingram and Shurin 2009). However, despite the quite trivial notion that all organisms can consume and/or can be consumed by other organisms, and that these trophic interactions generally depend on traits (e.g., Crawley 1989, Diaz et al. 2001), no study has ever simultaneously investigated within-community trait similarity patterns of two or more coexisting, interacting trophic levels. We thus still do not know how relevant such trophic interactions are in explaining trait similarity patterns within communities. Therefore, in this study we investigate whether trait-similarity patterns of communities of different trophic levels respond similarly to environmental gradients and whether trait variation patterns of one trophic level can result in similar patterns in another trophic level.

When studying such questions with a multitrophic approach, we suggest that it is better to replace the concept of abiotic filtering with fundamental niche filtering as the process that restricts trait ranges in communities. This is because in herbivores and predators, the availability of resources (food types, which are often not abiotic) can impose important restrictions on the fundamental niche of a species, restricting the set of species that can competitively interact in communities. In addition, the realized niche of species is generally not only restricted by competition filters, but can also be limited by predation filters. So from a multitrophic perspective, we suggest that dispersal, fundamental niche, competition, and predation filters interact within and across trophic levels (Fig. 1B).

In this multitrophic perspective, different fundamental niche filters can operate on the community assembly of different taxonomic or trophic groups, even in the same environment (Fig. 1B). For example, low soil pH may filter out some plant species that cannot tolerate soil acidity, while not directly acting upon herbivore community assembly. On the other hand, certain disturbances, such as traffic noise, can have a large impact on animals, but not on plants.

In addition, the assembly processes on different trophic levels may interact (Fig. 1B), where the resulting trait patterns of communities of one trophic level affect the community assembly of other trophic levels. These interactions can have different directions, where alternative hypotheses have analogies to classic food web theories on top-down vs. bottom-up regulation of populations. Filters on plant community assembly can be the structuring force, where the resulting plant trait variation imposes various filters (arrows HE₁–HE₄ in Fig. 1B) on possible herbivore traits. This we term the bottom-up control hypothesis of community assembly. For example, environments with infertile soils can filter out plant species that demand high nutrient levels for

their leaves. The resulting plant community then filters out small herbivore species that require high quality leaves (bottom-up restriction of trait expansion patterns). On the other hand, in areas where light competition results in plant species with a high spacing in leaf size, allometric scaling laws predict similar spacing patterns in the body size of herbivores (Ritchie and Olff 1999), providing a hypothetical example of bottom-up control of trait dispersion patterns. Alternatively, filters on herbivore community assembly can determine which plant species with which traits can occur in the community (arrows PL₁–PL₄ in Fig. 1B), which we call the top-down control hypothesis of community assembly. For example, the proximity of rivers or lakes can determine whether herbivores, like hippo, requiring the vicinity of water, can persist in a certain area. The resulting herbivore communities will filter out tall plant species (top-down effects on trait expansion patterns; Diaz et al. 2001). The top-down control of trait *dispersion* patterns is also possible, as multiple (e.g., different-sized) herbivores can suppress superior light competitors and thereby promote the coexistence of plant species with different traits (Olff and Ritchie 1998). Similar arguments can be developed for how interactions between herbivores and predators affect trait-based community assembly, and for indirect interactions between predator and plant traits (Fig. 1B). In line with classical theory, it is also possible that fundamental niche filters on different trophic levels are mostly abiotic in nature (e.g., frost) and overrule the importance of trophic interactions in determining community assembly (all feed-back arrows in Fig. 1B are unimportant), which we term the environmental control hypothesis of community assembly.

Here, we investigate the within-community trait expansion and dispersion patterns of two trophic levels, grasses (Poaceae, focusing on aboveground traits) and co-occurring herbivorous grasshoppers (Acrididae), over a rainfall and fire frequency gradient in a South African savanna landscape. The aim of this study is to investigate (1) whether and how within-community trait similarity patterns differ between grasses and grasshoppers, (2) how their trait similarity patterns affect each other (top-down vs. bottom-up), and (3) whether and how trait similarity varies along environmental gradients (environmental control). In this, we are able to compare the results of the classic approach of studying how abiotic and biotic filters affect community assembly with our novel multitrophic framework.

METHODS

Study area

Field work was carried out in Hluhluwe-iMfolozi Park (HiP), an 89 665-ha nature reserve in Kwazulu-Natal, South Africa (Appendix A: Fig. A1). This park is characterized by a high local and regional habitat heterogeneity, consisting of a mosaic of closed forests, open *Acacia* woodlands, bunch grasslands, and grazing

lawns (Whateley and Porter 1983, Owen-Smith 2004). This heterogeneity results from gradients in altitude (ranging from 50 to 500 m), rainfall (ranging from 650 mm/yr to 985 mm/yr in the higher altitude areas), fire frequency (mean fire return intervals 2–6 yr), hydrology, and soil heterogeneity (Appendix A: Figs. A2 and A3). Grass height is mainly determined by the interplay between fire, grazing by ungulates, and soil fertility (Cromsigt and Olff 2008).

Throughout the park, 50 10×10 m grassland plots with a woody coverage below 15% were chosen that together spanned the whole rainfall and fire frequency gradients. The plots were at least 25 m away from each other and were therefore considered to be independent replicates (see further documentation of this assumption in Appendix A). In these plots, we performed a one-time sampling of all grass and herbivorous species and we measured vegetation height. Fieldwork was carried out from April through June 2008.

Environmental data

Rainfall data from January 2001 through December 2007 from 17 rain gauge stations more or less evenly distributed across the study area were used to construct an annual amount of rainfall map with the Kriging interpolation method, which takes spatial covariance of rainfall patterns into consideration. The Kriging interpolation was performed using the four nearest rain gauge stations in Arc-GIS v 9.3.1 (ESRI, Redlands, California, USA; for the map, see Appendix A: Fig A2). GIS data about the fire frequency on a 200×200 m scale were available through digitized fire maps that were annually drawn between 1956 and 2004 by the park management authorities (Appendix A: Fig A3).

Grass and grasshopper data

Within each plot, the canopy height (i.e., height of highest leaf) of the grass layer was measured at one location in which the height was more or less equal to other places in the plot, and therefore representative. Vegetation height measurements were rounded to tens of centimeters, unless the height was lower than 5 cm, in which case height was rounded to 2.5 cm. Furthermore, five flowering individuals from each grass species were picked for the measurement of grass height, leaf surface area (LA), and specific leaf area (SLA) in the HiP Research Station. These traits were chosen because they represent different allocation strategies to drought stress (LA; Givnish 1987), relative growth rate (SLA), and competitive ability for light (height; Weiher et al. 1999), and because they have been shown to respond to community assembly processes (e.g., Anderson et al. 2011).

At the HiP research station, the canopy height of individual grasses was measured following Cornelissen et al. (2003). Leaf material was taken to the Groningen University (Netherlands). There, leaf blades were rewet between two pieces of tissue paper. After rewetting,

leaves were put on a scanner together with a black reference square (3×3 cm) for calibration. The surface area (LA) of the leaves was measured with the software package ImageTool v3 (UTHSC, Antonio, Texas, USA). Afterward, the leaves were dried in an oven at 70°C for at least 24 h. After one day of cooling, the leaf mass was measured with a scale to 0.001 g precision and SLA (cm^2 leaf/g leaf) was calculated.

Within the same plots, adult grasshoppers of the family Acrididae were collected with sweep nets for 15 minutes and taken to the HiP research station for species identification and morphological measurements.

In the HiP Research Station, grasshoppers were identified to species level and digital photographs were of the grasshoppers together with a ruler for calibration. The ImageTool v3 software was used to measure total body length and wing length. Relative wing length of each grasshopper species was calculated by taking the unstandardized residuals from a regression analysis with species wing length as the response variable and species total body length as the predictor variable. Positive residuals thus indicated a relatively large wing length, while negative residuals indicated a relatively small wing length. Total body length and relative wing length were chosen, because these traits reflect variation in diet requirements and resource partitioning (total body length; Belovsky 1997) and energy allocation to dispersal or stress avoidance (wing length; Harrison 1980).

Within-community trait similarity

Grand mean trait values of species were used for calculating within-community trait similarity patterns. This assumes that there are significant intrinsic species differences, which was indeed the case with, depending on the trait, between 47% (grass LA) and 83% (grasshopper body length) of the total variation explained by species identity. For both grasses and grasshoppers, the scaled observed trait range (OTR, highest minus lowest observed species trait value divided by the mean trait value) was calculated for each trait within each plot. Furthermore, we calculated the observed trait evenness (OTE) for each trait within each plot. OTE was defined as $1/(\text{sdT} + 1)$ in which sdT is the standard deviation of distances between adjacent trait values. It was therefore a measure for the evenness of differences between adjacent co-occurring trait values, with values close to zero indicating a very low evenness and a value of one indicating maximum evenness. To test whether the OTR and OTE values in plots were higher or lower than expected by chance, i.e., under- or overexpanded (trait range) or under- or overdispersed (trait evenness), we used two different null models. To study trait expansion, we performed 10 000 random draws from the species pool (see Fig. 2A, top right) without replacement, at each observed species richness. The species pool was defined as all the species sampled in this study. The chance of drawing a certain species

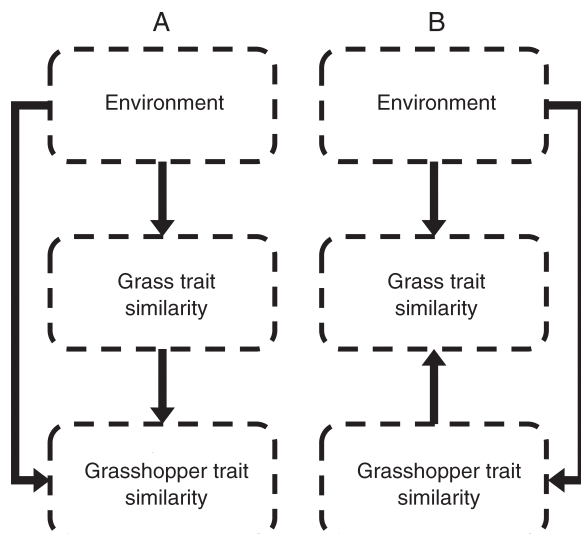


FIG. 2. Hypothesized relationships between environmental gradients and within-community grass and grasshopper trait similarity patterns. Arrows indicate causal relationships; boxes indicate major categories of variables. (A) In the bottom-up control model, within-community grass trait similarity (either expansion or dispersion) patterns are affected by the abiotic environment, while within-community grasshopper trait similarity patterns are affected by both the abiotic environment and grass trait similarity patterns. (B) In the top-down control model, within-community grass trait similarity patterns are affected by both the abiotic environment and within-community grasshopper trait similarity patterns. Within-community grasshopper trait similarity patterns are only affected by the abiotic environment.

from the species pool was proportional to the number of plots in which it occurred, to prevent false positives caused by an over-representation of rare species with extreme trait values in the randomized communities. Of the 10 000 random draws performed at each species richness, we calculated the mean scaled randomized trait range (RTR). Unscaled residual trait range (ReTR) or trait expansion for each plot was defined as: $\text{ReTR} = \text{OTR} - \text{RTR}$, in which RTR is the randomized trait range for random draws with the same richness as in the observed plot. Positive ReTR values thus indicated trait overexpansion (i.e., a higher within-community trait range than expected by chance), while negative values indicated trait underexpansion.

In the second null model, we took 10 000 random community draws under constrained conditions for each plot. From the species pool (again defined as all the species observed during this study), $S - 2$ (in which S is the observed species richness of the plot) species with trait values that fell within the unscaled observed trait range were selected. Again, the chance of a species being selected for the random community was proportional to its relative frequency in the species pool. Furthermore, the species with the highest and lowest trait value in the given observed community were also present in the randomized community. This way, we constructed new

random communities in which the species richness and trait range remained the same as in the observed communities, while the distances of trait values within that range could change (bottom right part of Fig. 1A). Then we calculated the average trait evenness of the 10 000 random draws for each plot (randomized trait evenness or RTE). For each plot, unscaled residual trait evenness (ReTE) or trait dispersion was calculated with the formula $\text{ReTE} = \text{OTE} - \text{RTE}$. Positive ReTE values thus indicated trait overdispersion (i.e., a higher within-community trait evenness than expected by chance), while negative values indicated trait underdispersion.

Finally, a Wilcoxon signed-rank test was used to test for overall significance of trait expansion and dispersion across plots. All calculations and the construction of null models were performed with R 2.9.2 (R Development Core Team 2009). For a more detailed description of the development of the null models and the assumptions underlying them, see Appendix B. For the R scripts for calculating ReTR and ReTE, see the Supplement.

Identifying drivers of trait similarity patterns

For both trait expansion and trait dispersion (residual trait range and residual trait evenness), two a priori chosen competing conceptual path models (or construct models, which represent theoretical hypotheses without all the mechanistic details) were developed: the bottom-up control model and the top-down control model (Fig. 2). In the bottom-up control model, the abiotic environment affects the grass trait similarity patterns, while grasshopper trait similarity patterns are affected by both the abiotic environment and grass trait similarity patterns (Fig. 2A). Thus, the bottom-up control model tested for both bottom-up processes and environmental control processes explaining variation in trait similarity patterns. In the top-down control model, grass trait similarity patterns are affected by both the abiotic environment and by grasshopper trait similarity, while grasshopper trait similarity patterns are only affected by the abiotic environment (Fig. 2B). Thus, the top-down control model tested for both top-down processes and environmental control processes explaining variation in trait similarity patterns.

Structural equation models (SEMs; Grace 2006, Grace et al. 2010) were run to test the fit of the construct models with the Amos 17.0 software package (Arbuckle 2007) using a maximum likelihood approach. These models were used because they allow for the testing of both direct and indirect effects of landscape variables on trait similarity patterns (Grace et al. 2010). Furthermore, because of their multivariate nature, in which most variables affect and are being affected by several other variables, with SEMs one can compare the strength and significance of opposite pathways (see, e.g., Grace et al. 2007), which allowed, in our case, comparing the relative strength of bottom-up and top-down processes in community assembly. In total, we ran

TABLE 1. Overall patterns in grass and grasshopper trait range and evenness relative to null models.

Trait	ReTR			ReTE		
	Plots > 0	<i>P</i>	Interpretation	Plots > 0	<i>P</i>	Interpretation
Grass						
LA	19	0.006	underexpansion	32	0.018	overdispersion
SLA	13	0.001	underexpansion	19	0.049	underdispersion
Height	20	0.005	underexpansion	22	0.743	
Grasshopper						
Length	20	0.244		21	0.463	
Relative wing size	14	0.251		25	0.824	

Notes: “Plots > 0” indicates the number of plots (out of 50 total) in which the observed trait range or evenness was lower than the average of 10 000 random draws with the same species richness. *P* values in boldface type indicate a significant pattern (Wilcoxon signed-rank test). Abbreviations are: LA, leaf area; SLA, specific leaf area; ReTR, residual trait range; ReTE, residual trait evenness.

four models: a bottom-up control model describing how trait expansion patterns of grasshopper communities are driven by trait expansion patterns in plant communities (bottom-up control model for trait expansion), the competing top-down model for trait expansion, in which grass trait expansion patterns were affected by grasshopper trait expansion patterns, and an equivalent bottom-up and top-down control model for explaining community trait dispersion patterns. We chose to do the analyses for trait expansion and dispersion patterns separately, because these trait similarity variables represent separate (relatively independent) ecological mechanisms. Furthermore, we chose to keep our saturated SEMs relatively simple to minimize the risk of overfitting (see for Appendix C for a more elaborate discussion on this choice). However, to test for the robustness of the models with expansion and dispersion analyzed separately, we also ran a bottom-up control model and a top-down control model with all trait similarity variables included (shown in Appendix C).

As environmental variables, we included the average amount of rainfall per year and fire frequency. As the grass variables, we used the ReTR or ReTE of grass LA, SLA, and canopy height. Furthermore, we included vegetation height in the models. As the grasshopper variables, we used ReTR or ReTE of grasshopper length and relative wing size. We started our analyses with saturated models, in which all grass and grasshopper variables were predicted by the environmental variables and in which all grasshopper variables were predicted by all grass variables (bottom-up control models), or vice versa (top-down control models). Furthermore, in the saturated models, fire frequency was predicted by the annual amount of rainfall. For a graphical overview of the models, see Fig. C1 and C2 in Appendix C. Starting with the saturated models, we developed final models using the following stepwise procedure: (1) correlations significantly improving the fit of the model based on a modification index above 4.0 were added; (2) paths with *P* values above 0.05 (χ^2 test) were omitted; and (3) variables that were not causally connected with any other variable were omitted. Our final models thus only

contained significant paths between variables. Overall model fit was assessed using the χ^2 statistic and the associated *P* value. Overall model fit was considered adequate if the associated *P* value was above 0.05, indicating that the null hypothesis (i.e., the SEM) could not be rejected. AIC values were then used to compare the fit of competing final models (i.e., bottom-up and top-down control models). For the paths of the final SEM explaining variation in trait expansion patterns, we then tested with simple *t* tests whether the paths linked with trait expansion patterns were due to either a relationship between the predictor value and (1) the maximum value or (2) the minimum value of the given trait. Thereby we investigated whether the predictor value either constrained the upper or lower limit of the given trait in local communities.

Furthermore, we also ran multiple regression models with grass and grasshopper trait expansion and dispersion variables as the response variables and rainfall and fire frequency as the predictor variables, to compare our SEM results with results from more traditional approaches (for more details, see Appendix D).

RESULTS

In total, we found 41 grass species and 53 grasshopper species across our 50 plots. Species richness ranged from 3 to 13 species per plot for grasses, with a median value of 7, and from 3 to 16 species per plot for grasshoppers, with a median value of 7.

Overall trait expansion and dispersion patterns

Across our 50 sampling locations, observed LA, SLA, and grass canopy height values had significantly lower ranges than communities from the null model. Therefore these traits were underexpanded, or, in local communities, overall less variable (difference between lowest and highest trait value) than expected from random community assembly (Table 1). We found significant overdispersion across our plots (Table 1) for grass height values, indicating limiting similarity. Within-community SLA values were significantly underdispersed (Table 1). Observed within-community LA dispersion patterns did

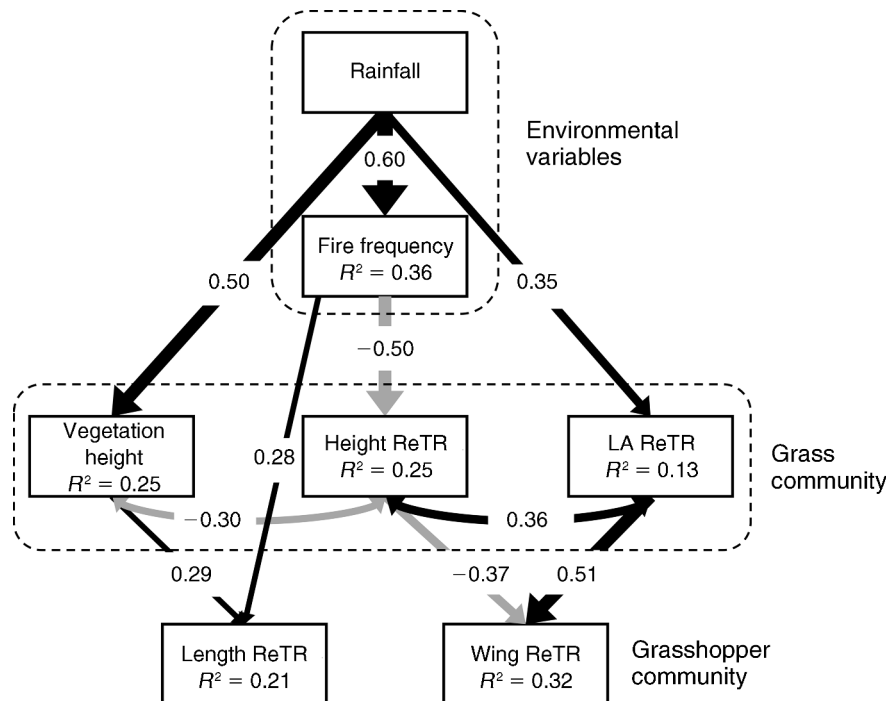


FIG. 3. Final model ($\chi^2 = 5.957$, $df = 11$, $P = 0.876$, $AIC = 39.957$) explaining the trait range expansion of grasses and grasshoppers, after the nonsignificant paths were omitted. Single-arrow connectors represent direct effects of one variable on another, while double-arrow connectors represent correlations. The thickness of the arrows indicates the interaction strength. Numbers on the connectors indicate the standardized regression or correlation coefficients, for single- and double-arrow connectors, respectively. Black paths indicate positive effects, while gray paths indicate negative effects. The R^2 value indicates the total proportion of variation of the given variable that could be explained by the model. ReTR stands for residual trait range or trait expansion; LA stands for leaf area.

not differ from the null model (Table 1). Furthermore, neither of the grasshopper traits showed within-community expansion or dispersion patterns differing from random community assembly (Table 1).

Structural equation models

For explaining variation trait expansion patterns across sites, the final bottom-up control model (Fig. 3; Appendix C for statistics of all paths) is the model that fitted the data best ($AIC = 39.957$, $\chi^2 = 5.957$, $P = 0.867$ vs. $AIC = 42.159$, $\chi^2 = 10.169$ and $P = 0.601$ for the final top-down control model). This model shows that variation in grass traits could mainly attributed to environmental differences across sites. Vegetation height

increased with annual amount of rainfall. Also LA trait expansion increased with rainfall, due to a relatively higher increase of maximum LA values than minimum LA values in communities (Table 2). Height trait expansion decreased with fire frequency (Fig. 3), due to a stronger increase of the mean grass height relative to the range in grass height with higher fire frequencies (Table 2).

We found that variation across sites in grasshopper trait expansion was mostly bottom-up regulated by grass variables and mostly indirectly regulated by environmental variables. Grasshopper body length trait expansion increased with vegetation height and fire frequency, due to an increase of maximum body length values with

TABLE 2. Results of t tests to show, for each path explaining a trait expansion pattern in Fig. 3, whether this pattern is caused by response in maximum trait values or in minimum trait values in communities to a change in the predictor variable.

Path	Minimum value			Maximum value		
	b	t	P	b	t	P
Rainfall \rightarrow LA ReTR	0.004	3.510	< 0.001	0.021	5.452	< 0.001
Fire frequency \rightarrow height ReTR	1.344	3.862	< 0.001	1.351	4.601	< 0.001
Fire frequency \rightarrow length ReTR	-0.031	-0.734	0.466	0.833	4.145	< 0.001
Vegetation height \rightarrow length ReTR	0.004	0.470	0.641	0.170	4.361	< 0.001
Height ReTR \rightarrow wing ReTR	2.756	1.540	0.130	-6.722	-2.328	0.024
LA ReTR \rightarrow wing ReTR	-3.365	-2.004	0.051	8.282	3.128	0.003

Note: Regression coefficients (b) are included.

vegetation height and fire frequency (Table 2). Relative wing size trait expansion increased with LA trait expansion and decreased with grass height trait expansion, since maximum relative wing size values were highest in areas with a high LA trait expansion and a low grass height expansion (Table 2).

Variation in trait dispersion across sites was similarly explained by the final bottom-up and top-down control model (Fig. 4; Appendix C for statistics of all paths) (AIC = 14.582, $\chi^2 = 2.582$, $P = 0.630$). The SEMs show that grasshopper body length dispersion was positively affected by annual rainfall, while grasshopper relative wing size dispersion is negatively correlated with SLA trait dispersion (Fig. 4).

In addition, we developed two saturated SEMs (bottom-up and top-down control) that simultaneously included trait expansion *and* dispersion variables (Appendix C: Figs. C5 and C6). Of these two models, the final bottom-up control SEM of trait similarity patterns performs best and shows qualitatively the same results as the previous SEMs (Appendix C: Fig. C7). This suggests that the SEMs, in which dispersion and expansion patterns were analyzed separately, produced robust conclusions.

The SEM results yielded different outcomes than traditional approaches, in which grasshopper body length expansion was best explained by fire frequency ($t = 2.570$, $P = 0.013$), grasshopper wing expansion by rainfall ($t = 2.371$, $P = 0.022$), grasshopper body length dispersion by rainfall ($t = 3.530$, $P < 0.001$), and grasshopper wing could not be explained by any of the environmental variables (Appendix D).

DISCUSSION

Our data provide the opportunity to evaluate if the proposed multitrophic framework of trait-based community assembly leads to different conclusions than analyses based on the classic idea of abiotic and competitive filters within trophic levels. We therefore tested if trophic interactions are additionally important in trait-based community assembly. According to classic trait-based community assembly theory (without trophic interactions), trait underexpansion patterns are expected in communities that are mainly structured by abiotic filtering, while trait overdispersion is expected when competition is important (Cornwell and Ackerly 2009). When using the standard analyses as used in other studies, we found significant underexpansion patterns for all grass traits but not for grasshopper traits, while significant overdispersion patterns were hardly found. This would suggest that abiotic filtering was the most important process in structuring grass communities, with only a limited role for interspecific competition in community assembly, and no explanation for observed within-community grasshopper trait similarity patterns. Furthermore, traditional multiple regression analyses that tested for effects of variation in environmental variables on grasshopper trait similarity patterns sug-

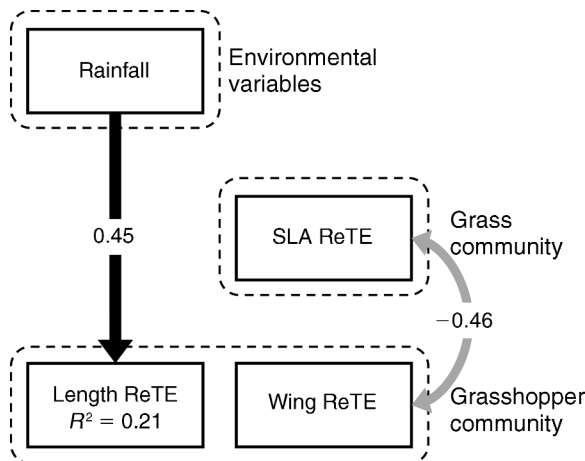


FIG. 4. Final model ($\chi^2 = 2.582$, $df = 4$, $P = 0.630$, AIC = 14.582) explaining the trait dispersion of grasses and grasshoppers, after the nonsignificant paths were omitted. Single-arrow connectors represent direct effects of one variable on another, while double-arrow connectors represent correlations. The thickness of the arrows indicates the interaction strength. Numbers on the connectors indicate the standardized regression or correlation coefficients, for single- and double-arrow connectors, respectively. Black paths indicate positive effects, while gray paths indicate negative effects. The R^2 indicates the total proportion of variation of the given variable that could be explained by the model. SLA stands for specific leaf area.

gested that variation between sites in within-community grasshopper trait similarity patterns were directly driven by variation in rainfall and fire frequency. However, we also used multivariate SEM analyses as a statistical method to test for the importance of trophic interactions in community assembly. This showed that variation in grass trait expansion patterns were explained by rainfall and fire, while grasshopper trait expansion patterns were largely explained by vegetation structure and grass expansion patterns (supporting the bottom-up control hypothesis of community assembly) and therefore only indirectly by environmental gradients. This shows the importance of trophic interactions on trait-based community assembly, and that our SEM analyses provide conclusions that cannot be picked up with the classic methods of analysis used in the literature so far.

Given the nature of our study system, it was to be expected that bottom-up controls (plant trait distributions determine grasshopper trait distributions) were more important than top-down effects. Previous work has shown the importance of fire, large mammalian herbivores, and rainfall in regulating plant community composition (e.g., Cromsigt and Olff 2008) and furthermore, invertebrate herbivores generally have a lower impact on plant communities than vertebrate herbivores (Crawley 1989) and are often bottom-up regulated (e.g., Haddad et al. 2001). However, our main objective was to show that trophic interactions next to environmental factors can affect the trait distribution on different trophic levels. The overall importance of top-down vs.



PLATE 1. Grassland in the northern part of Hluhluwe-iMfolozi Park, where the average annual amount of rainfall of over 750 mm, is among the wetter places in the area. Vegetation height was relatively high at these wet sites. Photo credit: F. van der Plas.

bottom-up controls on trait distributions at different trophic levels would require extensive meta-analyses of data from different ecosystems.

As our SEMs showed, trait expansion patterns in grasses were determined by environmental factors. These environmental factors can drive the observed trait expansion patterns in the grasses in different ways. In accordance with other studies, plant trait ranges became less constrained in more “benign” environments: LA expansion became larger in high-rainfall areas in accordance with Cornwell and Ackerly (2009). In dry areas, only species with small leaves occurred, while both species with large and small leaves occurred in high-rainfall areas. Large leaves evaporate relatively more water (Givnish 1987) and therefore our results are possibly the outcome of the inability of species with large leaves to survive in dry, low-rainfall areas. Fire had a negative effect on the canopy height trait expansion of the grasses. This is in line with Pausas and Verdu (2008), who showed that fire reduced trait space in Mediterranean tree communities. The limited range in grass canopy height values in areas that burn relatively frequently can possibly be explained by the fact that only tall grass species occur in such areas, which have a higher root/shoot ratio (T. M. Anderson, B. Kumordzi, W. Fokkema, H. Valls-Fox, and H. Olff, *unpublished manuscript*), allowing them to resprout after fires. The more constrained range in grass trait values in the more stressful dry and frequently burnt areas suggests that in those areas, fundamental niche filtering through abiotic conditions is important, only allowing those species that can persist drought and fire.

Trait variation in grasshoppers, on the other hand, seemed to be more structured by trophic interactions and only indirectly by environmental gradients. Grasshopper body length expansion was highest in areas with a tall vegetation (see Plate 1). While less attractive for large mammalian grazers, these areas seem to support the highest quantities of food for grass-feeding grasshoppers. Relatively large insect species also require relatively large quantities of food (Belovsky 1997) and could thus be filtered out in areas with low vegetation height and low food availability. The resulting pattern of relatively high trait expansion patterns in areas with a high vegetation and low trait expansion patterns in areas with a low vegetation is an example of a bottom-up process, in which the plant community imposes a fundamental niche filter on grasshoppers (arrow HE₃, Fig. 1). But an alternative explanation is that in areas with short vegetation, relatively large and conspicuous grasshoppers are more vulnerable to avian predators preferring to hunt in open vegetation, thereby excluding large species (Belovsky et al. 1990). That would be an example of a bottom-up process in which the local plant community, by forming certain structures, imposes a predation filter on the herbivore community (arrow HE₁, Fig. 1). Grasshopper wing expansion was highest in areas with a high grass LA expansion. LA has been suggested to be low in nutrient poor sites (Givnish 1987), and areas with a high LA expansion could thus be seen as areas with a high variation in resource quality for herbivorous insects. Some grasshopper species have strong preferences for high quality food, while other species can digest lower quality food as well (Behmer

and Joern 2008). In areas with a high variation in food quality, no single food type dominates, so that more selective species should be able to disperse when their food source has been depleted, while this ability to disperse is not needed for more generalist species. Species with relatively long wings are often good dispersers (Wootton 1992), while species with short wings are not. In areas with a high variation in vegetation quality or LA, one can thus expect a high variation in grasshopper wing length as well, while in other areas only species with relatively short wings occur. This would be another example of a plant community imposing a fundamental niche filter on herbivores (arrow HE₃, Fig. 1), interacting with dispersal filters. Surprisingly, we found that expansion of relative wing length was lowest in areas with a high expansion of grass canopy height, where mainly relatively short-winged grasshoppers occur (Table 2). A possible explanation for this may be the following. Expansion in relative wing length of grasshoppers may be seen as variation in ability to disperse. Low expansion may thus be caused by a lack of species with good dispersal ability, since species with a high relative wing length were rare in areas where grass height trait expansion was high. High expansion of grass canopy height implies high structural complexity of the vegetation, which is in general beneficial for food availability of insects (Haddad et al. 2001). Species with low dispersal ability or low relative wing length may therefore be expected to dominate in such favorable habitats.

We hardly found evidence for trait overdispersion for grasshopper or aboveground grass traits. Overdispersion is expected to arise from interspecific competition and the consequent resource partitioning between species within communities (Cornwell and Ackerly 2009). This would imply that grasses in this savanna do not compete very strongly with each other. Competition between grasses and trees in savannas has been extensively investigated, and has yielded important functional differences that may promote their coexistence, such as rooting depth, fire tolerance, and access to nutrients (Scholes and Archer 1997, Cramer et al. 2010). However, the importance of competition in relation to trait differentiation between different grass species in savannas has been much less investigated. Furthermore, our analyses are based on aboveground grass traits and will thus be most relevant for light competition. As the grass layer in our study system is often kept low by mammalian herbivores and frequent fires, it can be understood why light competition is not a main factor in structuring these plant communities. Belowground competition among grasses probably plays a more important role, which would require the investigation of belowground traits (rooting depth, specific root length, mycorrhizal associations, and so on). However, such traits are not directly, and therefore probably also less strongly, linked to grasshopper community assem-

bly than aboveground grass traits. Therefore, it is not surprising that the multivariate multitrophic analyses did not show strong direct links between the trait dispersion of grasses and grasshoppers.

In summary, we conclude that the effects of environmental gradients on within-community trait similarity patterns can be direct or indirect, mediated by interactions among trophic levels. With our multitrophic conceptual framework for trait-based community assembly (Fig. 1B) and our SEM approach, we could elucidate which candidate variables were the direct and indirect predictors of trait similarity patterns of coexisting grass and grasshopper communities, showing that trophic interactions were more important than environmental control in explaining trait similarity patterns in grasshopper communities.

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SUPPLEMENTAL MATERIAL

Appendix A

Description of the study area and the sampling locations (*Ecological Archives* E093-074-A1).

Appendix B

Detailed description of null model development plus a discussion of the assumptions and their link with theory (*Ecological Archives* E093-074-A2).

Appendix C

Detailed description of structural equation model (SEM) development, plus a discussion of the assumptions of the SEMs presented in the main text and extra SEM results, not shown in the main text (*Ecological Archives* E093-074-A3).

Appendix D

Traditional multiple regression analyses showing how trait similarity patterns change over environmental gradients (*Ecological Archives* E093-074-A4).

Supplement

R script files to calculate trait expansion and dispersion patterns, a community composition matrix input file, and a species traits input file for both R scripts (*Ecological Archives* E093-074-A5).